

Electroantennogram responses of the oriental fruit fly, *Dacus dorsalis*, to a spectrum of alcohol and aldehyde plant volatiles

Douglas M. Light & Eric B. Jang

USDA-ARS, Western Regional Research Center, 800 Buchanan Street, Albany, CA 94710, and USDA-ARS, Tropical Fruit and Vegetable Laboratory, P.O. Box 4459, Hilo, HI 96720, U.S.A.

Accepted: March 30, 1987

Key words: Diptera, Tephritidae, oriental fruit fly, *Dacus dorsalis*, fruit, green-leaf volatiles, olfaction, electrophysiology, electroantennogram

Abstract

Electroantennograms (EAGs) were recorded from unmated, laboratory-reared, male and female oriental fruit flies, *Dacus dorsalis*, in response to a range of between C₁ and C₁₂ carbon chain-length saturated and unsaturated aliphatic alcohols and aldehydes, most all of which are known host-plant volatiles. Only two of the 35 compounds tested elicited significantly larger EAGs from female than male antennae. For the two functional-group series tested, aldehydes elicited responses greater than or equal to the responses to the alcohols. In general, the unsaturated alcohols did not elicit responses significantly different from the saturated alcohols. However, the unsaturated aldehydes, (E)-2-hexenal and 10-undecenal, elicited larger amplitude EAGs than their saturated analogs. EAGs were significantly greater for a particular carbon chain-length, with responsiveness to primary alcohols peaking at C₆ and aldehydes peaking at C₇. The (E)-2- monoenic alcohols peaked at C₆, while the (E)-3-alcohols plateaued between C₅ and C₈. The greatest EAG responses of all compounds tested were elicited by the saturated and unsaturated C₆ alcohols and aldehydes which are constituents of the "general green-leaf volatile complex" that emanates from most plants. The potential adaptive benefit of selective sensitivity to green-leaf volatiles is discussed in regards to foraging behaviors of oriental fruit flies.

Introduction

The chemoreception of host-plants is fundamental to the biology of phytophagous insects (Dethier, 1982; Schoonhoven, 1968, 1981), though present knowledge is limited as to the specific volatile chemical constituents which contribute to the olfactory aspect of host-plant recognition (Finch, 1980; Visser, 1986). The odor of a plant is typically composed of tens to nearly hundreds of components, many relatively unique though others extremely common (see Van Straten & Maarse, 1983, for fruit and vegetable volatiles and Visser *et al.*, 1979, for leaf volatiles).

The most frequently identified class of plant volatiles is the ubiquitous "general green-leaf volatile complex", (G.L.V.C.), which contributes to a variable extent to the leaf and fruit odors of numerous plants. Derived from the oxidative fragmentation of the plant fatty acids, linoleic and linolenic acids, the G.L.V.C. is composed of the six-carbon aldehydes: hexanal, (Z)-3-hexenal, and (E)-2-hexenal; and the six-carbon alcohols: hexan-1-ol, (Z)-3-hexen-1-ol, and (E)-2-hexen-1-ol (Visser *et al.*, 1979; Buttery, 1981). Qualitatively, the specific composition of the blend of leaf alcohols and aldehydes has been found to vary between plant species; while quantitatively,

the relative contribution of the G.L.V.C. to a plant odor ranges from minor to major for intact plant tissue, but is enhanced substantially when the plant tissue is damaged releasing oxidative enzymes (Visser *et al.*, 1979; Buttery, 1981).

Recently, Visser (1983, 1986) reviewed electrophysiological studies on plant-odor reception and found that components of the G.L.V.C. dominate the selectivity of populations of plant-odor receptors on adult antennae of the oligophagous insects tested. In addition, the antennae of the Mediterranean fruit fly, *Ceratitidis capitata* (Wiedemann) have recently been found to also be selectively responsive to the green-leaf six-carbon alcohols and aldehydes over analogs of other chain-lengths (Light *et al.*, in press).

The stimulatory potency of the "general green-leaf volatiles" is further explored here, testing the antennal olfactory receptivity of another tephritid species, the oriental fruit fly, *Dacus dorsalis* Hendel. *D. dorsalis* is a polyphagous (over 150 host plant species) frugivorous pest, which is sympatric and resource competitive with *C. capitata* throughout much of their tropical and subtropical Pacific basin range (Bess, 1953; Christenson & Foote, 1960; Haramoto & Bess, 1970; Bateman, 1972; Wong *et al.*, 1983, 1985). We recorded electroantennograms from both male and female laboratory-reared *D. dorsalis* in response to a spectrum of saturated and unsaturated aliphatic primary alcohols and aldehydes to determine the olfactory selectivity of their antennae.

Materials and methods

Insects. Pupae of *D. dorsalis* were obtained from a laboratory colony maintained at the USDA, Tropical Fruit and Vegetable Research Laboratory, Honolulu, Hawaii. Upon their arrival, pupae were sexed and placed in separate cages. After eclosion, adult flies were provided sucrose cubes, hydrolyzed protein and water until testing two to five days postemergence.

Olfactory stimuli. Table 1 lists the compounds tested, their supply sources and purities. The compounds were dissolved in spectrometric grade hexane (that was additionally distilled and treated with an

antioxidant) at a rate of one part test compound and nine parts hexane solvent, forming 10% volume per volume solutions. From these solutions, test cartridges were produced for each compound by pipetting 1 μ l aliquots onto separate 1 \times 2 cm pieces of fluted, glass-fiber filter paper, which were then inserted into individual Pasteur pipets. Before or during each experiment, new cartridges were loaded with compound, individually sealed in zip-lock plastic bags and placed in a freezer (-4°C) and then transferred to a fume hood just prior to testing.

Electrophysiological recording technique. Electroantennogram (EAG) techniques used here are a modification of previous techniques utilizing glass capillary Ag-AgCl electrodes filled with insect saline (Schneider, 1957; Light, 1983; Light *et al.*, in press). Intact flies were immobilized in a Plexiglass block by a yoke. The recording electrode was inserted into the distal region of the terminal antennal segment or funiculus, while the indifferent electrode was positioned into the hemocoel of the cranial activity. The signal was amplified 100X by a Grass P-16 microelectrode amplifier and viewed on either an analog (Tektronix 5113) or digital (Nicolet 4094) storage oscilloscope. EAG deflections were measured directly from the stored screen image or from either photographs (Tektronix C5-A camera, Polaroid-type 667 film) or digital graphs from an X-Y plotter (Hewlett Packard 7475A).

Odor delivery. The odor delivery system and stimulation technique were essentially the same as that described by Light (1983) and Light *et al.* (in press). In brief, a constant flow (1.0 liter/min) of charcoal-filtered and humidified compressed air was passed over the antennae through a disposable nozzle (automatic pipet tip, Centaur Chemical) positioned ca. 1 cm from the antenna. When activated by a timing circuit, a three-way solenoid valve diverted the purified air through the stimulus cartridge where evaporating volatiles were picked up and carried into the nozzle and then onto the antenna. Stimulus duration was 1.0 sec. The order of presentation of test compounds was randomly assigned. Because of the variation in volatility of test compounds, only relative comparisons can be made between the odorous

Table 1. Source and purity of chemicals used in electrophysiological studies and their presence in a variety of host fruits of *Dacus dorsalis*.

Compound	Chemical Purity (%) ^a	Presence in fruit of:						
		Source ^b	Citrus ^{c,d}	Guava ^d	Papaya ^c	Passion fruit ^d	Peach ^d	Plum ^d
Aliphatic alcohols								
Methanol	100.0	A	+	+	+	+	+	+
Ethanol	100.0	A	+	+	+	+	+	+
Propan-1-ol	95.0	B	+		+	+		+
2-Propen-1-ol	99.0	C						
Butan-1-ol	100.0	D	+		+	+	+	+
(E)-2-Buten-1-ol	92.3	B						+
3-Buten-1-ol	99.1	D						
Pentan-1-ol	99.5	D	+	+	+	+	+	+
(E)-3-Penten-1-ol	97.0	C						
Hexan-1-ol	100.0	D	+	+	+	+	+	+
(E)-2-Hexen-1-ol	95.9	D	+		+		+	+
(Z)-2-Hexen-1-ol	99.5	D						
(E)-3-Hexen-1-ol	100.0	D				+		+
(Z)-3-Hexen-1-ol	99.9	D	+	+	+	+		+
Heptan-1-ol	98.0	D	+		+	+		+
Octan-1-ol	100.0	D	+	+	+	+	+	+
(E)-2-Octen-1-ol	92.0	C						
(E)-3-Octen-1-ol	84.7	C				+		
Nonan-1-ol	100.0	D	+	+				+
Decan-1-ol	99.0	D	+					
Undecan-1-ol	96.5	B	+					
Dodecan-1-ol	96.9	F	+				+	
Aliphatic aldehydes								
Propanal	54.0	B						
Butanal	67.0	B	+	+			+	
(E)-2-Butenal	93.9	E						
Pentanal	99.0	D	+	+				
Hexanal	98.3	D	+	+			+	+
(E)-2-Hexenal	98.6	D	+	+			+	+
Heptanal	98.1	D	+				+	
Octanal	95.5	D	+					
Nonanal	91.1	F	+				+	+
Decanal	97.9	D	+					
Undecanal	91.0	D	+					
10-Undecenal	85.0	D						
Dodecanal	89.5	G	+					

^a Capillary GLC analysis (12.5 m × 0.2 mm Methyl Silicone cross-linked column) at USDA-ARS-WRRC, Albany, CA; ^b A, U.S. Industrial chemicals; B, Eastman Kodak Co.; C, synthesized at USDA-ARS-WRRC, Albany, CA; D, Aldrich Chemical Co.; E, Chem Service, Inc.; F, Fritzsche, Dodge and Olcott, Inc.; G, source presently unknown, from file at USDA-ARS-WRRC, Albany, CA; ^c Kefford and Chandler (1970); ^d various references in Van Straten and Maarse (1983); ^e Flath and Forrey (1977).

stimuli. A period of greater than 90 sec of clean air both preceded and followed each stimulation, which was found to be more than adequate for complete recovery.

Experimental procedure. For each stimulus, EAGs were recorded from at least five flies of each sex. "Control" stimulations (using filter papers either untreated or impregnated with 1 μ l of the hexane sol-

vent) and "standard" stimulations (using fresh cartridges impregnated with 1 μ l of 1% hexane-1-ol) were interspersed *ca.* every fifth to tenth stimulation.

EAGs to test compounds were evaluated by measuring the maximum amplitude of negative deflection ($-mV$) elicited by a given stimulus, and then subtracting the amplitude of the response to the accompanying solvent control. The millivolt responses to all compounds were converted to percentage values of the response to the accompanying 1% hexan-1-ol standard, as used in other EAG studies on insect olfaction (Dickens, 1984; Dickens & Boldt, 1985; Light *et al.*, in press). This normalization of each response to a percentage of standard response allowed for comparison of responses within and between preparations (Payne, 1975). Also this procedure minimizes the observed variability in: 1) absolute responsiveness between preparations, 2) order of presentation of compounds and 3) the time dependent variability in antennal responsiveness (Light, 1983; Dickens, 1984). Mean responses were compared using and the nonparametric Mann-Whitney U test (Snedecor & Cochran, 1967).

Results

Mean EAG responses of female and male antennae to the hexan-1-ol standard were not significantly different ($p = 0.11$), (-1.58 mV (SE = 0.24 mV) and -1.25 mV (SE = 0.11 mV) for five females and males, respectively). Furthermore, while slight variation in sexual responsiveness to most of the other test odorants was observed, in response to only two compounds were significant differences in EAG amplitude found between the sexes.

Saturated primary alcohols. For the series of saturated primary alcohols tested, the antennae of both male and female oriental fruit flies were most responsive to hexan-1-ol (Fig. 1). As chain-length of the saturated alcohols both increased and decreased from six-carbons, the antennal responsiveness steadily declined, forming a broad and steep bell-shaped response distribution. The only exception from this progressive decline in responsiveness was the significantly lower responsiveness to butan-1-ol relatively

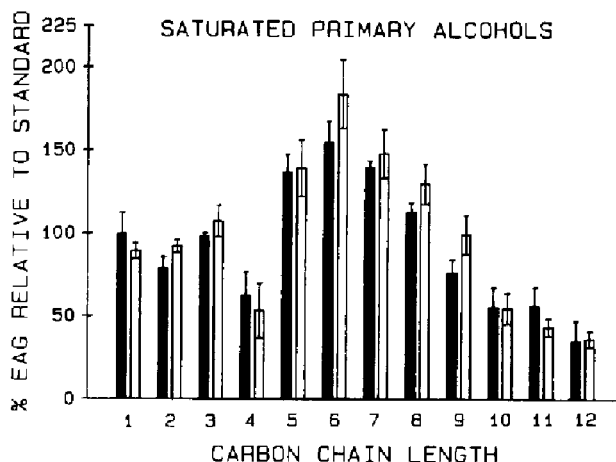


Fig. 1. Mean EAG responses of ♀ (filled bars) and ♂ (blank bars) *D. dorsalis* to 1 μ l doses of 10% solutions (v/v) of saturated primary alcohols of various carbon chain-lengths. Vertical lines: S.E.M., $n = 5$, and a 100% response is approx. -1.6 mV for ♀♀ and -1.3 mV for ♂♂.

to higher responsiveness to methanol, ethanol and propan-1-ol.

Unsaturated primary alcohols. Antennal responsiveness peaked at C_6 for the series of (E)-2-unsaturated primary alcohols tested (Fig. 2). However, for the limited series the (E)-3-en-1-ols tested, antennal responsiveness reached a plateau at

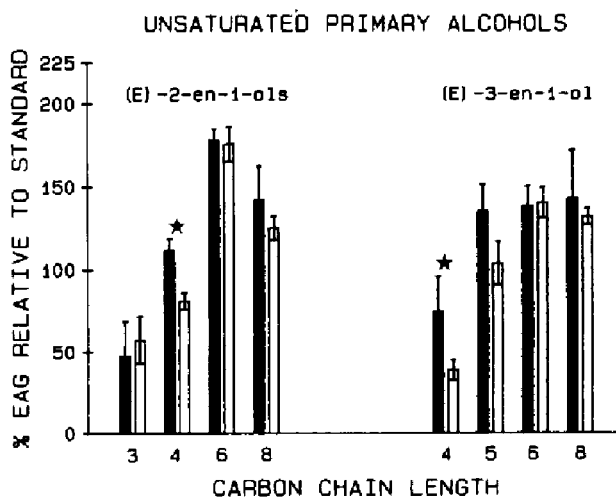


Fig. 2. As Fig. 1, but mean EAG responses of unsaturated (E)-2- and (E)-3- primary alcohols of various carbon chain-lengths. Stars: significant differences in responsiveness between sexes.

C₆ and C₈ for males and C₅, C₆ and C₈ for females. The only significant differences in antennal responsiveness between the sexes observed in this study were the greater responses of female than male antennae to (E)-2-buten-1-ol ($p < 0.01$) and (E)-3-buten-1-ol ($p < 0.05$). Comparing the EAGs between the unsaturated alcohols that varied only in position of the *trans* double-bond, (E)-2-hexen-1-ol elicited significantly greater responses in both sexes ($p < 0.02$) than the (E)-3-hexen-1-ol isomer, as did (E)-2-buten-1-ol over its (E)-3-isomer for males ($p < 0.01$). There was no difference in response to the (E)-2- and (E)-3-octen-1-ol isomers.

When both the (Z) and (E) geometric isomers of both hex-2-en-1-ol and hex-3-en-1-ol were tested, the naturally-occurring (E)-2- and (Z)-3-isomers elicited, with one exception, only slightly, but not significantly greater, EAGs than their geometric or positional isomers (Fig. 3). For both sexes, the one exception was the significantly greater ($p < 0.04$) EAGs to (E)-2-hexen-1-ol than to its geometric isomer, (Z)-2-hexen-1-ol.

Only two of ten unsaturated alcohols elicited significantly different EAGs from their saturated alcohol analogs. Significantly greater ($p < 0.03$) EAGs were elicited by propan-1-ol than by 2-propen-1-ol for both sexes, and by (E)-2-buten-1-ol than by butan-1-ol for females.

Saturated aldehydes. The antennae of both male and female *D. dorsalis* were moderately responsive to the full-range of saturated aliphatic aldehydes tested

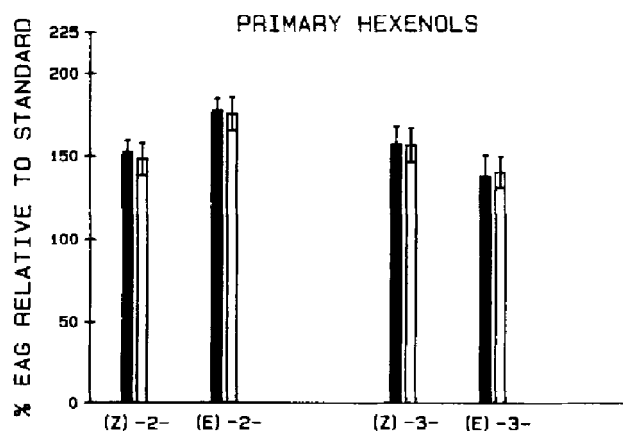


Fig. 3. As Fig. 1, but mean EAG responses of primary hexenols.

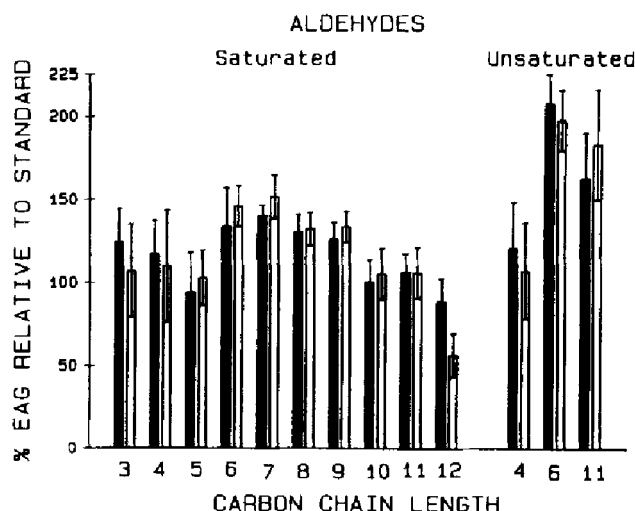


Fig. 4. As Fig. 1, but mean EAG responses of saturated aldehydes of various carbon chain-lengths and the unsaturated aldehydes, (E)-2-butenal, (E)-2-hexenal and 10-undecenal.

(Fig. 4). The antennal responsiveness to the aldehyde series had a more gradual sloping distribution with a plateau between C₆ and C₉, and a maximum at C₇. As carbon chain-length increased or decreased beyond C₆–C₉, responsiveness did not diminish but remained at an intermediately high level from C₁₀ to C₁₁ and C₅ to C₃.

Unsaturated aldehydes. EAGs for both sexes of *D. dorsalis* were significantly greater ($p < 0.03$) for both (E)-2-hexenal and 10-undecenal over their unsaturated aldehyde analogs, while butanal and (E)-2-butenal were equally stimulatory (Fig. 4). Furthermore, of all the compounds tested on antennae of *D. dorsalis*, (E)-2-hexenal and 10-undecenal elicited the largest EAGs.

Alcohol vs. aldehyde responsiveness. The type of functional group present on a particular chain-length molecule had a significant affect on antennal responsiveness. The aldehyde moiety elicited significantly greater ($p < 0.02$) EAGs than the alcohol functional group for carbon chain-lengths of four, and nine through eleven for both sexes of *D. dorsalis*, and C₁₂ for females. Conversely, only one alcohol exceeded its aldehyde analog, with pentan-1-ol eliciting greater EAGs than pentanal ($p < 0.03$) in male oriental fruit flies.

Discussion

Effects on EAG responsiveness

Sexuality. Among the 35 compounds tested, sexually dimorphic responses were found for only two compounds, (E)-2- and (E)-3-buten-1-ol, where in both cases female antennae were more responsive than male antennae. Conversely, the general uniformity between the sexes in EAG-plant volatile responsiveness of oriental fruit flies suggests a common ecological need for olfactory discrimination and assessment of host plants and/or habitat by both sexes. Once arriving at a plant, males and females might utilize the perceived resource in either a similar manner, e.g. foraging for food (plant-sap, nectar, honeydew, protein, etc.), or a dissimilar manner, e.g. as an aggregation or "calling" site for males or as an ovipositional site for females.

In other tephritid species, sexual dimorphism in EAGs to plant volatiles has either not been found, as with *Rhagoletis pomonella* (Fein *et al.*, 1982) and *Dacus oleae* (Van der Pers *et al.*, 1984) or is of a limited nature as found both here and with *C. capitata* (Light *et al.*, in press).

Carbon chain length. Oriental fruit fly antennae are selectively most responsive to six and seven carbon, and to a lesser extent five and eight carbon, saturated and unsaturated chain-lengths for the series of alcohol and aldehyde functional groups tested. Though the full range of ca. C₂ to C₁₂ alcohols and aldehydes are frequently reported to be components of numerous host and non-host fruits (Van Straten & Maarse, 1983), it is the C₆ and C₇ compounds that elicit the greatest EAGs in *D. dorsalis*, i.e. stimulate the greatest proportional number of acceptors.

Similar EAG selectivity findings have been recently reported on a wide phylogenetic range of insects (Visser, 1986). The most stimulatory chain-length of saturated primary alcohols found in EAG studies has also been C₆ for *Leptinotarsa decemlineata* (Visser, 1979), *Rhynchaenus quercus* (Kozłowski & Visser, 1981), *Anthonomus grandis* (Dickens, 1984), *Sitobion avenae* (Yan & Visser, 1982) and *C. capitata* (Light *et al.*, in press). Similarly, hexanal was the most potent of a series of saturated aldehydes tested

on antennae of *L. decemlineata* (Visser, 1979), *R. quercus* (Kozłowski & Visser, 1981) and *C. capitata* (Light *et al.*, in press). However, a majority of the EAG-plant volatile studies have found that responsiveness to aldehydes peaks at heptanal, with a ranking for most species of C₇ > C₈ > C₉ > C₆ (for Diptera: *C. capitata*, *D. oleae* and *Rhagoletis cerasi*. Guérin *et al.*, 1983a; *Psila rosae*, Guérin & Städler, 1982 and Guérin *et al.*, 1983b; and *Delia antiqua*, Guérin & Städler, 1982; for Lepidoptera: *Yponomeuta* spp., Van der Pers, 1981; and for Coleoptera: *A. grandis*, Dickens, 1984; and *Trirhabda bacharides*, Dickens & Boldt, 1985).

Unsaturation. Studies of EAG response selectivity in insects have all found that responses to certain monoenic alcohols, aldehydes and acetates exceed those of their saturated analogs (see above references and Visser, 1983 and 1986). Recent EAG experiments on medflies (Light *et al.*, in press) concur with this finding. Oriental fruit flies were also found to have higher responsiveness to a few unsaturated over saturated aldehydes (i.e. (E)-2-hexanal and 10-undecenol). However, oriental fruit flies have no significant differential responsiveness to the saturation or unsaturation of most alcohols tested. The only other exception reported has been the onion fly, *D. antiqua*, which has a significantly greater response to hexan-1-ol than to various isomeric hexen-1-ols (Guérin & Städler, 1982).

Functional groups. For *D. dorsalis* antennae, aldehydes either equal the potency (C₅–C₈) or exceed the potency (C₄, C₉–C₁₂) of alcohols of the same chain-length and saturation. The occurrence of greater (or statistically equal) responsiveness to aldehydes over alcohols has been reported for other tephritids, *C. capitata* (Light *et al.*, in press; Guérin *et al.*, 1983a), *D. oleae* and *R. cerasi* (Guérin *et al.*, 1983a); and similarly for other Diptera though the series of reported aldehydes and alcohols tested only ranged between C₆ to C₉ (*P. rosae*, Guérin & Visser, 1980; Guérin & Städler, 1982, and Guérin *et al.*, 1983b; and *Delia brassicae*, Guérin & Städler, 1982). In the case of other insect species, where series of alcohols and aldehydes have been tested, EAG amplitudes have been selectively greatest for either alde-

hydes (*A. grandis*, Dickens, 1984 and *T. bacharides*, Dickens & Boldt, 1985); or alcohols (*D. antiqua*, Guérin & Städler, 1982; *L. decemlineata*, Visser, 1979; *R. quercus*, Kozłowski & Visser, 1981; and *Adoxophyes orana* and various *Yponomeuta* species, Van der Pers, 1981).

Comparing the relative EAGs of the oriental fruit fly vs. the Mediterranean fruit fly, it appears that *D. dorsalis* antennae have a greater responsiveness than *C. capitata* antennae to both short-chain alcohols (ethanol and propan-1-ol) and aldehydes (propanal, butanal and pentanal), along with the longer chain-length undecanal. On the other hand, *C. capitata* antennae generally exceed *D. dorsalis* antennae in responsiveness to the (E)-2- and (E)-3-unsaturated alcohols tested, except for the hexen-1-ols. Presently it is unknown, and far too speculative without supporting behavioral experiments to state, whether such apparently minor differences in antennal responsiveness between these sympatric species could, for example, give *D. dorsalis* a resource competitive edge over *C. capitata*, as observed in competitive ecological displacement of *C. capitata* by *D. dorsalis* in the lower elevations of the Hawaiian islands (Bess, 1953; Haramoto & Bess, 1970; Vargas *et al.*, 1983; Wong *et al.*, 1983, 1985).

General green-leaf volatiles. The fifteen compounds that evoke the greatest EAGs from *D. dorsalis* antennae are ranked in the following hierarchy: (E)-2-hexenal > (E)-2-hexen-1-ol \geq 10-undecenal \geq hexan-1-ol \geq (Z)-3-hexen-1-ol \geq (Z)-2-hexen-1-ol \geq heptan-1-ol = heptanal \geq (E)-3-hexen-1-ol \approx hexanal \approx (E)-3-octen-1-ol = (2)-octen-1-ol \approx pentan-1-ol = octanal \approx (E)-3-penten-1-ol. Components of the G.L.V.C. dominate this EAG responsiveness ranking (four of the top five compounds). Along with plant species-specific blends of important discriminatory "key compounds" (often terpenes and their analogs), the green-leaf volatiles have been shown to dominate the EAG responsiveness of oligophagous insect antennae over aldehydes and alcohols with shorter or longer carbon chain-lengths (see for review, Visser, 1983, 1986; e.g. *P. rosae*, Guérin & Visser, 1980; *D. antiqua* and *D. brassicae*, Guérin & Städler, 1982; *Metasyrphus venabiles*, Hood Henderson & Wellington, 1982; *L. decem-*

lineata, Visser, 1979; *R. quercus*, Kozłowski & Visser, 1981; *A. grandis*, Dickens, 1984; *T. bacharides*, Dickens & Boldt, 1985; and *Yponomeuta* spp. and *A. orana*, Van der Pers, 1981).

Thus, oriental fruit flies have antennae "selectively-tuned" for reception of the green-leaf C₆ alcohols and aldehydes, and thereby, have large populations of responsive acceptors, that proportionally may exceed the sensory endowment for reception of other compounds and semiochemicals (Jang and Light, unpubl.). It is now apparent that not only monophagous (e.g. *T. bacharides*, a weed bio-control candidate, Dickens & Boldt, 1985) and oligophagous insect species (see above references and Visser, 1983 & 1986), but also polyphagous insects, such as *D. dorsalis*, *C. capitata* (Light *et al.*, in press) and *Locusta migratoria* (Visser, 1983), might have a considerable sensory capability for the selective reception of the constituents of the G.L.V.C.

The plant volatiles that have been identified as kairomonal attractants to date (see Finch, 1980; Visser, 1986) are relatively host-species or host-genera unique "key" compounds that often surpass the green-leaf volatiles in eliciting the largest EAGs. Whether *D. dorsalis* or other tephritid fruit flies are attracted to constituents or blends of the general green-leaf odor is uncertain. However, other plant and fruit constituents are attractive to tephritids; e.g. the attraction of: *D. dorsalis* males to methyl eugenol (Howlett, 1915; Steiner, 1952) and males or females to 16 of 232 botanical extracts (Keiser *et al.*, 1975), *C. capitata* males to (+)- α -copaene (Jacobson *et al.*, 1984; Teranishi *et al.*, 1986) and females to 61 of 232 botanical extracts (Keiser *et al.*, 1975), and *R. pomonella* to various apple esters (Prokopy *et al.*, 1973; Fein *et al.*, 1982; Reissig *et al.*, 1982).

Although there is evidence that certain insect species discriminate in their behaviors between different green-odor blends (see Visser, 1986), it remains unlikely that the qualitative presence of "green-leaf volatiles" alone could as a class of plant compounds serve a herbivore in its discrimination of host from non-host plants because of the ubiquitous release of these catabolic products from plant parenchyma. On the other hand, the large sensory investment in reception of the "green-leaf volatiles" has probably been evolutionarily selected for (or not against) and

most likely remains adaptive in *D. dorsalis*, *C. capitata* and other insects. The reception of "green-leaf volatiles" by *D. dorsalis* and other tephritids may be fundamental to such short and/or long range appetitive behaviors that occur on foliage and fruits; such as foraging for water, food and shelter, and the establishment and subsequent attractiveness of male calling and courtship sites. It remains possible that the more universal plant olfactory cues, i.e. the G.L.V.C., might influence or promote these discriminative searching behaviors, because oriental fruit flies are readily observed foraging on both host and non-host plants and trees (Christenson & Foote, 1960; Wong *et al.*, 1985). The perception of the complex host plant odor, or specific constituents thereof, by the insect's central nervous system is believed to initiate and maintain various searching or foraging behaviors, but not to guide or direct those orientations and taxes (Light, 1986). Visual optomotor anemotactic and/or phototelotactic orientation have been hypothesized to mechanistically guide these foraging behaviors in other tephritid species, e.g. *R. cerasi* (Levinson & Haisch, 1984), *R. pomonella* (Prokopy, 1986), and *C. capitata* (Féron, 1962; Nakagawa *et al.*, 1978).

Because of the selective receptivity to constituents of the G.L.V.C., we are presently exploring the influence of both constituents and the entire and properly-proportioned blend of green-leaf volatiles on various foraging behaviors of *D. dorsalis* and other tropical tephritids.

Résumé

Electroantennogrammes des réponses de Dacus dorsalis à une gamme d'alcools et d'aldéhydes de substances volatiles de végétaux

Des électroantennogrammes (EAG) ont enregistré les réponses, en élevages de femelles et mâles vierges de *Dacus dorsalis*, à une gamme de chaînes de carbones de C₁ à C₁₂ saturés et non-saturés d'alcools aliphatiques et d'aldéhydes, dont beaucoup sont connus comme substances volatiles des végétaux. Seulement 2 des 35 composés examinés ont provoqué des EAG significativement plus importants chez les femelles que chez les mâles. Pour les séries des

deux groupes fonctionnels examinés, les aldéhydes ont provoqué des réponses supérieures ou égales aux alcools. En général, les réponses aux alcools non-saturés n'étaient pas significativement différentes des réponses aux alcools saturés. Cependant, les aldéhydes non-saturés, (E)-2-hexénal et 10-undécénal, ont induit des EAG de plus grande ampleur que leurs analogues saturés. Les EAG étaient significativement les plus importants pour une chaîne de longueur particulière, la réponse aux alcools primaires culminant en C₆ et les aldéhydes en C₇. Les alcools monoéniques (E)-2- culminaient en C₆, tandis que les alcools (E)-3- étaient égaux entre C₅ et C₈. Les EAG les plus importants ont été obtenus pour tous les composés examinés avec les alcools et aldéhydes en C₆ qui appartiennent à "l'odeur verte complexe" émise par beaucoup de plantes. Le bénéfice adaptatif potentiel de la sensibilité sélective à "l'odeur verte" des feuilles est examinée en fonction du comportement de prospection de *D. dorsalis*.

Acknowledgements

The authors thank Janice Nagata, USDA-ARS, Hilo, Hawaii for assistance with the EAG recordings, and Drs. R. B. Buttery, H. T. Chan Jr., J. C. Dickens and D. McInnis for comments.

References

- Bateman, M. A., 1972. The ecology of fruit flies. *Ann. Rev. Ent.* 17: 493–518.
- Bess, H. A., 1953. Status of *Ceratitidis capitata* in Hawaii following the introduction of *Dacus dorsalis* and its parasites. *Proc. Hawaii. Ent. Soc.* 15: 221–234.
- Buttery, R. G., 1981. Vegetable and fruit flavors. In: *Flavor Research, Recent Advances*, (R. Teranishi, R. A. Flath & H. Sugisawa, eds.) Marcel Dekker, Inc., N.Y. pp. 175–216.
- Christenson, L. D. & Foote, R. H., 1960. Biology of fruit flies, *Ann. Rev. Ent.* 5: 171–192.
- Dethier, V. G., 1982. Mechanism of host-plant recognition. *Ent. exp. & appl.* 31: 49–56.
- Dickens, J. C., 1984. Olfaction in the boll weevil, *Anthonomus grandis* Boh. (Coleoptera:Curculionidae): electroantennogram studies. *J. Chem. Ecol.* 10: 1759–1785.

- Dickens, J. C. & Boldt, P. E., 1985. Electroantennogram responses of *Trirhuhda buchurides* (Weber) (Coleoptera: Chrysomelidae) to plant volatiles. *J. Chem. Ecol.* 11: 767–779.
- Dickens, J. C. & Payne, T. L., 1977. Bark beetle olfaction: Pheromone receptor system in *Dendroctonus frontalis*. *J. Insect Physiol.* 23: 481–489.
- Fein, B. L., Reissig, W. H. & Roelofs, W. L., 1982. Identification of apple volatiles attractive to the apple maggot, *Rhagoletis pomonella*. *J. Chem. Ecol.* 8: 1473–1487.
- Féron, M., 1962. L'instinct de reproduction chez la mouche méditerranéenne des fruits *Ceratitis capitata*. Comportement sexuel. Comportement de ponte. *Rev. Pathol. Veg. Entomol. Agr. Fr.* 41: 1–129.
- Finch, S., 1980. Chemical attraction of plant-feeding insects to plants. In: *Applied Biology Vol. V* (T. H. Coaker, ed.) Academic press, N.Y., pp. 67–143.
- Flath, R. A. & Forrey, R. R., 1977. Volatile components of papaya (*Carica papaya* L., Solo variety). *J. Agric. Food Chem.* 25: 103–109.
- Guérin, P. M. & Stadler, E., 1982. Host odour perception in three phytophagous Diptera – A comparative study. *Proc. 5th Int. Symp. Insect-Plant Relationships*, Wageningen, 1982. Pudoc, Wageningen, pp. 95–105.
- Guérin, P. M. & Visser, J. H., 1980. Electroantennogram responses of the carrot fly, *Psila rosae*, to volatile plant components. *Physiol. Ent.* 5: 111–119.
- Guérin, P. M., Remund, U., Boler, E. F., Katsyannos, B. & Delrio, G., 1983a. Fruit fly electroantennogram and behavior responses to some generally occurring fruit volatiles. *Proc. CEC and IOBC Int. Symp. Fruit Flies of Economic Importance*. Athens, Greece. 1982, pp. 248–251.
- Guérin, P. M., Stadler, E. & Buser, H. R., 1983b. Identification of host plant attractants for the carrot fly, *Psila rosae*. *J. Chem. Ecol.* 9: 843–861.
- Haramoto, F. H. & Bess, H. A., 1970. Recent studies on the abundance of the oriental and Mediterranean fruit flies and the status of their parasites. *Proc. Hawaii. Ent. Soc.* 20: 551–566.
- Hood Henderson, D. E. & Wellington, W. G., 1982. Antennal sensilla of some aphidophagous Syrphidae (Diptera): fine structure and electroantennogram study. *Can. J. Zool.* 60: 3172–3186.
- Howlett, F. M., 1915. Chemical reactions of fruit flies. *Bull. Ent. Res.* 6: 297–305.
- Jacobson, M., Uebel, E. C., Lusby, W. R. & Cunningham, R. T., 1984. Essential oil yields medfly attractant. *Chem. Engin. News* Dec. 17: 24.
- Kefford, J. F. & Chandler, B. V., 1970. Volatile flavoring constituents. In: *The Chemical Constituents of Citrus Fruits*. Academic Press, pp. 87–111.
- Keiser, I., Harris, E. J. & Miyashita, D. H., 1975. Attraction of ethyl ether extracts of 232 botanicals to oriental fruit flies, melon flies, and Mediterranean fruit flies. *Lloydia* 31: 141–152.
- Kozłowski, M. W. & Visser, J. H., 1981. Host-plant-related properties of the antennal olfactory system in the oak flea weevil, *Rhynchaeus quercus*. Electroantennogram study. *Ent. exp. & appl.* 30: 169–175.
- Levinson, H. Z. & Haisch, A., 1984. Optical and chemosensory stimuli involved in host recognition and oviposition of the cherry fruit fly, *Rhagoletis cerasi* L. *Z. angew. Ent.* 97: 85–91.
- Light, D. M., 1983. Sensitivity of antennae of male and female *Ips paraconfusus* (Coleoptera: Scolytidae) to their natural aggregation pheromone and its enantiomeric components. *J. Chem. Ecol.* 9: 561–583.
- Light, D. M., 1986. Central integration of sensory signals: an exploration of processing of pheromonal and multimodal information in lepidopteran brains. In: *Mechanisms in Insect Olfaction*. (T. L. Payne, M. C. Birch & C. E. J. Kennedy, eds.), Oxford University Press, Oxford. pp. 287–301.
- Light, D. M., Jang, E. B. & Dickens, J. C. Electroantennogram responses of the Mediterranean fruit fly, *Ceratitis capitata*, to a spectrum of plant volatiles. *J. Chem. Ecol.*, in press.
- Nakagawa, S., Prokopy, R. J., Wong, T. Y., Ziegler, J. R., Mitchell, S. M., Urago, T. & Harris, E. J., 1978. Visual orientation of *Ceratitis capitata* flies to fruit models. *Ent. exp. & appl.* 24: 193–198.
- Payne, T. L., 1975. Bark beetle olfaction. III. Antennal olfactory responsiveness of *Dendroctonus frontalis* Zimmerman and *D. brevicornis* Le Conte (Coleoptera: Scolytidae) to aggregation pheromones and host tree terpene hydrocarbons. *J. Chem. Ecol.* 1: 233–242.
- Prokopy, R. J., 1986. Visual and olfactory stimulus interaction in resource finding by insects. In: *Mechanisms in Insect Olfaction*. (T. L. Payne, M. C. Birch & C. E. J. Kennedy, eds.), Oxford University Press, Oxford. pp. 81–89.
- Prokopy, R. J., Moericke, V. & Bush, G. L., 1973. Attraction of apple maggot flies to odor of apples. *Environ. Ent.* 2: 743–749.
- Reissig, W. H., Fein, B. L. & Roelofs, W. L., 1982. Field tests of synthetic apple volatiles as apple maggot attractants. *Environ. Ent.* 11: 1294–1298.
- Schneider, D., 1957. Elektrophysiologische Untersuchungen von Chemo- und Mechanorezeptoren der Antenne des Seidenspinners *Bombyx mori* L. *Z. Vergl. Physiol.* 40: 8–41.
- Schoonhoven, L. M., 1968. Chemosensory bases of host plant selection. *Ann. Rev. Ent.* 13: 115–136.
- Schoonhoven, L. M., 1981. Chemical mediators between plants and phytophagous insects. In: *Semiochemicals, Their Role in Pest Control*. (D. A. Nordlund, R. L. Jones & W. J. Lewis, eds.), John Wiley & Sons, N.Y., pp. 31–50.
- Snedecor, G. W. & Cochran, W. G., 1967. *Statistical Methods*, 6th ed. Iowa State University Press.
- Steiner, L. F., 1952. Methyl eugenol as an attractant for oriental fruit fly. *J. Econ. Ent.* 45: 241–248.
- Teranishi, R., Buttery, R. G., Matsumoto, K. E., Stern, D. J., Cunningham, R. T. & Gothilf, S., 1986. Recent developments in chemical attractants for tephritid fruit flies. In: *Allelochemicals: Role in Agriculture, Forestry and Ecology*. (G. R. Walker, ed.), ACS Symp. Series. pp. 431–438.
- Van der Pers, J. N. C., 1981. Comparison of electroantennogram response spectra to plant volatiles in seven species of *Yponomeuta* and in the tortricid *Adoxophyes orana*. *Ent. exp. & appl.* 30: 181–192.

- Van der Pers, J. N. C., Hanriotakis, G. E. & King, B. M., 1984. Electroantennogram responses from olfactory receptors in *Dacus oleae*. *Entomol. Hellenica* 2: 47–53.
- Van Straten, S. & Maarse, H., 1983. Volatile Compounds in Food, 5th ed. Central Institute for Nutrition and Food Research TNO, Zeist, The Netherlands.
- Vargas, R. I., Harris, E. J. & Nishida, T., 1983. Distribution and seasonal occurrence of *Ceratitus capitata* (Wiedmann) (Diptera:Tephritidae) on the island of Kauai in the Hawaiian islands. *Environ. Ent.* 12: 303–310.
- Visser, J. H., 1979. Electroantennogram responses of the Colorado beetle, *Leptinotarsa decemlineata* to plant volatiles. *Ent. exp. & appl.* 25: 86–97.
- Visser, J. H., 1983. Differential sensory perceptions of plant compounds by insects. *Am. Chem. Soc. Symp. Ser. No. 208*: 215–230.
- Visser, J. H., 1986. Host odor perception in phytophagous insects. *Ann. Rev. Ent.* 31: 121–144.
- Visser, J. H., Van Straten, S. & Maarse, H., 1979. Isolation and identification of volatiles in the foliage of potato, *Solanum tuberosum*, a host plant of the Colorado beetle, *Leptinotarsa decemlineata*. *J. Chem. Ecol.* 5: 13–25.
- Wong, T. T. Y., Nishimoto, J. I. & Mochizuki, N., 1983. Infestation patterns of Mediterranean fruit fly and the oriental fruit fly (Diptera:Tephritidae) in the Kula area of Maui, Hawaii. *Environ. Ent.* 12: 1031–1039.
- Wong, T. T. Y., McInnis, D. O. & Mochizuki, N., 1985. Seasonal distribution and abundance of adult male oriental fruit flies (Diptera:Tephritidae) in Kula, Maui, Hawaii. *J. Econ. Ent.* 78: 1267–1271.
- Yan, F. & Visser, J. H., 1982. Electroantennogram response of the cereal aphid *Sitobion avenae* to plant volatile components. *Proc. 5th Int. Symp. Insect-Plant Relationships*. Pudoc, Wageningen, pp. 387–388.